Consequences of Supply-Side Ecology: Manipulating the Recruitment of Intertidal Barnacles Affects the Intensity of Predation Upon Them

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Abstract. An experimental manipulation of barnacles successfully recruiting to two seashores tested the consequences of these variations to predation by whelks and the eventual population structure of the barnacles. Very young barnacle spat were removed from some areas with and without predatory whelks. The whelks moved away from areas without the juvenile barnacles, but stayed and ate barnacles present on the treatment with barnacle recruitment. Predation resulted in almost complete elimination of the cohort of barnacles. In contrast, barnacles survived and grew to reproductive sizes on areas initially without whelks but with recruits. Because of the movements of whelks and their predation on the barnacles, the final abundances of whelks and barnacles in each plot bore little relationship to their initial experimental treatments. Thus caution is needed in interpreting the causes of static patterns of abundance in the field, where the processes involved earlier are not definitely known. These results point to a need to incorporate variation in recruitment into models of biological interactions.

Introduction

An important development in marine ecology within the last five years has been the reappraisal of the incidence and implications of variation in larval settlement and recruitment (Lewin, 1986; Young, 1987; Underwood and Fairweather, 1988). Biological oceanographers and fisheries scientists (*e.g.,* Thorson, 1950; Coe, 1953; Ricker, 1954; Beverton and Holt, 1957; Loosanoff, 1966) have long focussed on the settlement from the wa-

ter column of planktonic larvae of marine invertebrates and fishes, and their subsequent recruitment to adult populations (and hence to exploitable stocks). Field ecologists have recently turned their attention to the magnitudes of local variation in this recruitment (Victor, 1983; Caffey, 1985; Gaines and Roughgarden, 1985), and the consequences this has for diversity and abundance of marine species (Underwood and Denley, 1984; Connell, 1985; Peterson, 1986). This new emphasis has been termed "supply-side ecology" (Lewin, 1986). Specific theoretical models (Sale, 1982; Roughgarden, 1986; Menge and Sutherland, 1987) have been proposed incorporating such variation for the subsequent demography of these "open" populations and whether recruitment variation determines the size of populations. Variation in recruitment is considered an important alternative explanation for many ecological patterns (Underwood and Denley, 1984; Lewin, 1986). However, community ecologists have given less consideration to the consequences of this variation for biological interactions (such as predation or competition) among marine organisms (Underwood and Fairweather, 1988).

It has been shown experimentally that variation in the availability of different potential prey in a rocky intertidal area can greatly affect predation on them (Fairweather, 1985, 1987). One mechanism by which availability of prey might vary is via the settlement of their larvae and their recruitment as juveniles. In such circumstances, variation in the recruitment of particular prey species might also influence the outcome of predatory interactions and hence the structure of the community (Underwood and Fairweather, 1988). Although observations in other intertidal work suggest these effects (Fischer-Piette, 1935; Dayton, 1971; Menge, 1972; Morgan, 1972), no experiments involving manipulations of re-

cruitment have been done. Here I describe an experiment that simulat ___ ___ ilure of recruitment by an important memb___ ___ rocky intertidal community into areas with ar___ ___ nout predators on two seashores in New Sout___ ___ ___ Australia. Species considered were the barnacle ___ ___ ___ropora rosea (Krauss) and the muricid whelk *Morula marginalba* Blainville. *T. rosea* is the most abundant sessile animal at midtidal levels on shores exposed to wave action; *M. marginalba* is the most common predator in such areas (Denley and Underwood. 1979; Underwood. 1981a; Underwood *et al.*, 1983).

Materials and Methods

The experiment used simultaneous manipulations of recruitment and predation on small patches of rocky shore to test whether whelks are capable of responding to a simulation of an extreme case of recruitment variation. On some shores around Sydney, NSW, Australia (Underwood *et al.*, 1983), large areas of the midshore were devoid of nearly all animals that, prior to 1983, had supported dense populations of *Tesseropora* (from a settlement in 1978; Underwood and Denley, 1984) and their associated communities. The two seashores used were Green Point in Broken Bay (33°30' S, 151°17' E), and Maitland Bay (33°28' S, 151°22' E) on the open coast. I simulated the failure of barnacles to recruit by removing newly settled individuals surrounding selected pools on each shore. Two 400 m² sites at each of the two shores were chosen within which at least 24 slight depressions, pools, and small crevices could be found. All were separated by distances of at least 2 m. These crevices were suitable to shelter *Morula* (Moran, 1985), and a few animals had found refuge there. Around these pools were generally homogeneous bare areas of at least 1 m² with few prey (barnacles and gastropods) at a total density of only about 15 per m². In the first week of March, 1984, I noted a reasonably dense set of *Tesseropora* that had occurred about a week before at Maitland Bay (approximately 2000 per m²) and Green Point (1100 per m²). Spat at Green Point may have settled a week earlier than at Maitland Bay (pers. obs.).

At each site (two on each shore, consisting of 24 pools each), six pools were assigned to each of four treatments (see Fig. 1): a control with whelks and recruits present, a treatment with recruits removed but whelks present, a treatment with whelks absent, and a treatment with both whelks and recruits absent. Initially, the one- to two-week-old barnacle spat comprised some 98% of the potential prey on all plots although it is unusual for whelks to eat them so young; Fairweather, 1985). Barnacles were not seen being eaten by the whelks present at this time and probably very few were killed by predators during the first month (although mortality did occur). Barnacle
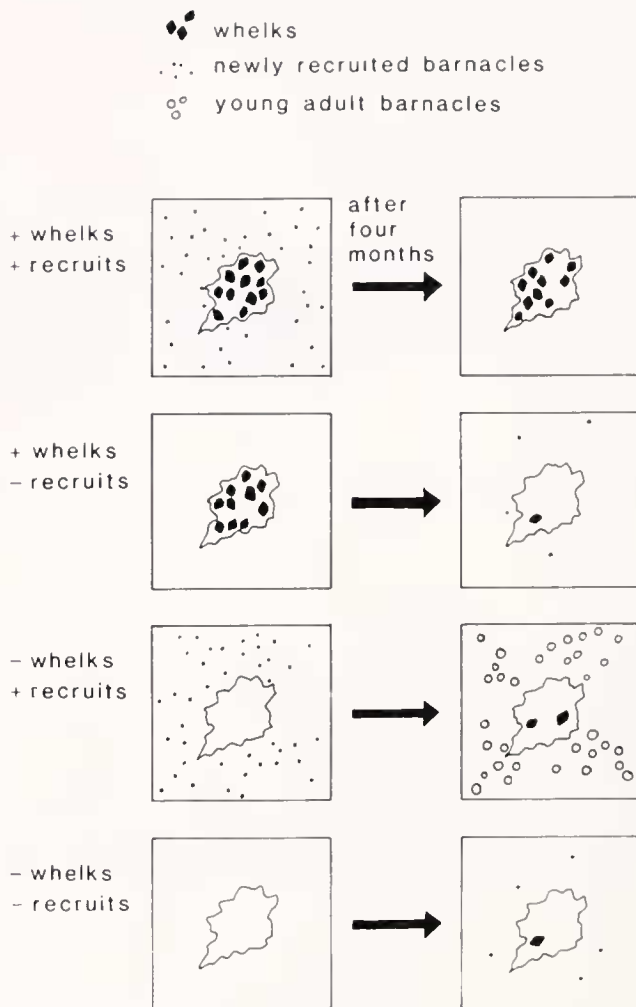

Figure 1. Pictorial representation of the initial and final configurations of the four treatments in the experiment. The whelks are shown hiding in the central crevice in each plot and the survival and growth of the barnacles is indicated by the number and sizes in each treatment (+whelks/+recruits are the control plots).

spat were removed from the appropriate plots by careful scraping with a knife on the 5th and 6th of March (so that <10% remained). The time taken to set this up, and to maintain and record these plots, prevented the use of more than one quadrat per treatment. Hence, each treatment pool was a replicate ($n = 6$, total sample size = 96). All whelks were removed from the study sites, and then fifty *Morula* (similar to the initial densities, see Fig. 2) were added to the 1-m² area surrounding each treatment pool with whelks.

The survivorship of recruits on a small (0.04 m²), permanent quadrat within each plot was recorded at monthly intervals. The number of whelks staying in each plot was also recorded. The experiment ran for 18 weeks. The numbers of barnacles at each sampling time were analyzed using a four factor (Shores, Sites within Shores,

Table I

Examples of. a) analysis of variance of the numbers of Tesseropora *at the final date* $n = 6$ *Sites is considered a random factor nested within Shores; other factors are considered fixed.* $NS = P > 0.05$

Source of variation	Degrees of freedom	Mean square	F-ratio	P	% of variation
Main Effects					
Shores, Sh	1	37	4	NS	0.8
Sites within Shores,					
Si(Sh)	2	10	1	NS	0.5
Predators, P	1	1204	143	<0.01	27.1
Recruits, R	1	771	1927	<0.001	17.3
Interaction					
Sh × P	1	88	11	NS	2.0
Sh × R	1	43	107	<0.01	1.0
Si(Sh) × P	2	8	1	NS	0.4
Si(Sh) × R	2	0	0	NS	0.0
P × R	1	1411	941	<0.001	31.7
Sh × P × R	1	81	54	<0.05	1.8
Si(Sh) × P × R	2	2	0	NS	0.1
Residual	80	10			17.4
Total	95				

b) Student-Newman-Keuls tests of mean numbers of barnacles surviving for the Sh × P × R interaction. "MB" = Maitland Bay, "GP" = Green Point, "+" = present, "−" = absent

Treatments								
Shore	MB	GP	GP	MB	GP	MB	GP	MB
Predators	−	−	+	+	−	−	+	+
Recruits	+	+	−	−	−	−	+	+
Means	18.5 >	12.3 >	2.8 =	2.5 =	2.1 =	2.0 =	1.3 =	0

Whelks, and Recruits), mixed model analysis of variance (after procedures in Underwood, 1981b) (see design in Table I). Differences among means were revealed by use of Student-Newman-Keuls tests on the means (Underwood, 1981b).

Results

Differences in the analyses among sites or shores are less relevant to the original hypothesis about recruitment, but may represent significant sources of variation in barnacle or whelk numbers. For example, in the final sample, Shores differed (see Tables 1, II) in that there were more surviving barnacles in the plots from which whelks had been removed at Maitland Bay than at Green Point (as might be expected from the starting numbers *i.e.*, Fig. 2). Sites within each shore were not divergent (*i.e.*, despite different numbers of recruits initially, the two sites at each shore yielded a similar result). The treatment with recruits, but without whelks, had more barnacles than all other treatments, and this treatment at Maitland Bay had more than the corresponding treatment at

Green Point (reflecting the initial numbers, see Table II, Fig. 2).

During the four-month experimental period, the number of whelks on plots declined rapidly where there were no recruits available as prey (Fig. 2a), while they did not move away from plots with juvenile barnacles. The whelks that disappeared were found in crevices outside the experimental plots and hence had not died. Thus, whelks responded readily and negatively to experimentally induced variation in recruitment of a major prey: the predators avoided the areas that simulated failures of recruitment.

Analyses of the number of barnacles present at the start of the experiment revealed significant differences between shores, and between plots where recruits were present and where they had been removed (see Tables I, II; Fig. 2b). In contrast, the final configuration of prey in plots was rather different from initial populations (Fig. 1). Numbers of recruits declined on all plots, but were annihilated by whelks (to local extinction at Maitland Bay and nearly so at Green Point; Fig. 2b). The rate of decline was greater at Maitland Bay. Some small recruitment (from the plankton) occurred subsequently on each shore, but at different times among the sites. After four months, there were again two statistically distinct groups of "barnacle" and "non-barnacle" plots, but densities of young *Tesseropora* in the controls had declined so much that these plots were indistinguishable from the "non-barnacle" group (Fig. 2b).

Discussion

The most direct test of whether variation in recruitment interacts with predation would include manipulation of the number of recruits to populations of prey and/or modifications of the timing of their arrival. Of course this would be difficult to do, especially regarding the timing of episodes of recruitment (because of uncertainty in the availability of larvae at any time). The plankton represents a "mystery stage" (Spight, 1975) in the life cycle of many marine organisms that is currently impossible to predict for these and other species (Underwood, 1979). The experiment used a somewhat less direct approach. By removing recruits as soon as they were observed, it was possible to create situations where a species had effectively "failed" to recruit, which could be compared to undisturbed areas with the "normal" number of recruits. This methodology is particularly applicable to sessile species such as barnacles, while it is difficult to increase the number of recruits to an area without great disturbance.

In this experiment, whelks left plots without recruits; *Morula* individuals migrated from unmanipulated areas without prey (Fairweather, 1988). These data suggest

Table II

Summary of anal___ ___ ___ ___ Juvenile barnacles in the experiment

Dat	Significant factors	Results
March (initial)	Shores	MB > GP
	Recruits	+r > −r (= zero)
April	Shores	MB > GB
	Whelks × Recruits	−w/+r > +w/+r > +w/−r = −w/−r (= zero)
May	Sites	(undefined spatial variation)
	Whelks	+w > −w
	Recruits	+r > −r
June	Shores × Whelks	MB/−w > GP/−w > MB/+w > GP/+w
	Shores × Recruits	MB/+r > GP/+r > MB/−r > GP/−r
July (final)	Shores × Whelks × Recruits	MB/−w/+r > GP/−w/+r > other treatments

"w" = whelks, "r" = recruits, "+" = present, "−" = absent, "MB" = Maitland Bay, "GP" = Green Point. Results of Student-Newman-Keuls tests of differences among means are also given.

that persistent, dense aggregations of whelks require the natural equivalent of the treatment with recruitment and whelks initially. Where whelks remained, the barnacles suffered greater mortality than in areas without whelks. Thus the four different initial treatments changed into three sorts of communities (Fig. 1). Plots from which barnacles had been experimentally removed finished with no or few barnacles or whelks. Control plots finished with whelks but few or no barnacles, while plots which started with only barnacles remained that way (with some thinning). Very few whelks located these plots (Fig. 2a). Although this pattern could change if later migrations of whelks located plots with surviving barnacles, the results suggest that persistent and dense populations of barnacles require the natural equivalent of the treatment with recruitment in the absence of whelks. This situation does occur on the coast of New South Wales, but the locations of such patches vary through time (Fairweather, 1988).

The final abundances of predators and prey in the experimental communities, however, gave little indication of the interaction of predation with recruitment (see Fig. 1). Without direct knowledge of these processes during the previous four months, the pattern of these divergent plots could be mistakenly attributed to many combinations of the success or failure of recruitment, the intensity of predation, and other factors (such as physical disturbance) not considered here. It would be perilous to interpret any extant pattern of abundance of prey as being the result of presently observable predatory interactions without experimental and historical evidence. Descriptive surveys of community structure cannot tell us much about the establishment and maintenance of these patterns (Wiens, 1981). Indeed, some observed interactions may constitute mere epiphenomena (Underwood et al., 1983; Sutherland and Ortega, 1986; Weinberg et al., 1986), in that any effects on demography and community relations of prey may be only transitory. The recent history of these processes acting on each site is important (Peterson and Black, 1988); to predict the abundance of either species in this experiment, the intensities of both processes involved must be known.

The consequences of this simulated recruitment failure go beyond direct effects on the demography of open populations (Roughgarden, 1986); variations in larval supply can set the scene for ecological interactions by determining the population sizes of the participants (Caffey, 1985). Most recent field studies concerning variation in the settlement, and subsequent recruitment, of planktonic larvae of benthic marine invertebrates have documented the magnitude of such variation (e.g., Caffey, 1985; Connell, 1985; Gaines et al., 1985; Peterson, 1986), or searched for its larger-scale oceanographic causes by looking at events in the plankton that influence the eventual numbers of recruits (e.g., Gaines and Roughgarden, 1987; Peterman and Bradford, 1987; Shanks and Wright, 1987). More attention should be paid to the consequences of recruitment variation instead of only concentrating on the causes.

This third avenue of research is suggested by the results here (see also Underwood et al., 1983; Sutherland and Ortega, 1986). We need to take variation in recruitment into account when considering possible outcomes of interactions like predation (Fairweather, 1985, 1987). There is a need for both theory and experiment incorporating variable recruitment in biological interactions as well as in demographic models, explicitly as a variable (Caffey, 1985; Underwood and Fairweather, 1988), not just characterized as consistently great or small (as in Roughgarden, 1986; Menge and Sutherland, 1987). In providing a variable input, recruitment has been shown here to influence the sorts of small scale interactions that organize intertidal assemblages.
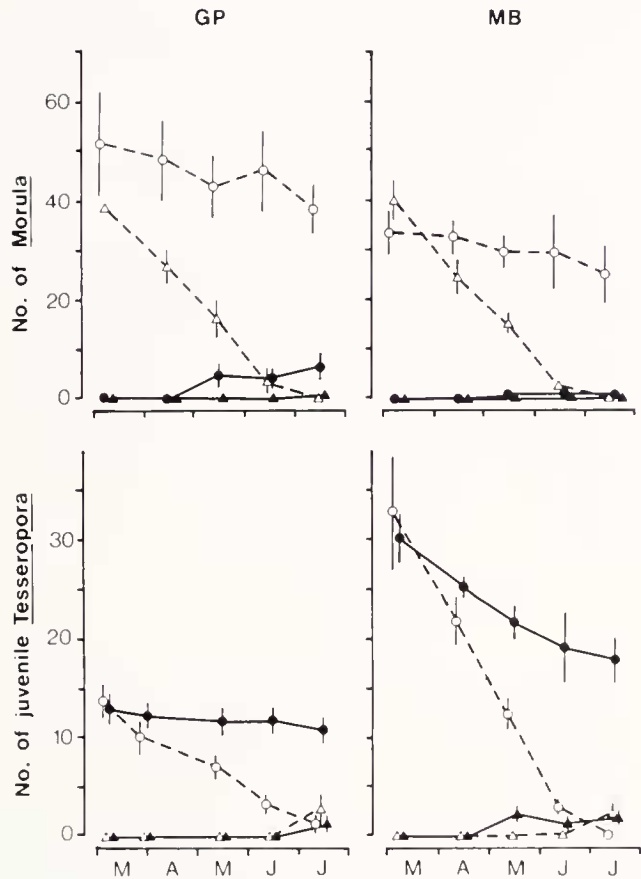
GP   MB

Figure 2. Densities of (a) whelks per m² and (b) barnacles per 0.04 m² during the experiment. GP denotes Green Point, MB = Maitland Bay, ○ = controls, ● = predators removed, △ = recruits removed, ▲ = predators and recruits removed. Means and their standard errors are shown as points and error bars, $n = 6$ replicate plots. Data for only one site are shown for each shore because the Sites factor was rarely significant in the analyses (see Table II).

Acknowledgments

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